1-1-2000

Small mammals in their environment: habitat selection in the context of landscape physiognomy and composition

Jessemine Lee-Saa Fung
Iowa State University

Small mammals in their environment: habitat selection in the context of landscape physiognomy and composition

by

Jessemine Lee-Saa Fung

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Major Professor: Brent J. Danielson

Iowa State University

Ames, Iowa

2000

Graduate College
Iowa State University

This is to certify that the Master's thesis of

Jessemine Lee-Saa Fung

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

TABLE OF CONTENTS

CHAPTER 1. GENERAL INTRODUCTION

Introduction

As we lose more contiguous natural habitats through anthropogenic processes, analyzing species movement patterns and behaviors is essential to interpreting their response to habitat fragmentation. Anthropogenic effects increase heterogeneity of natural habitats across space by degrading once-continuous natural habitats into remnant pieces (Diffendorfer et al., 1995). With the cultivation of native grasslands, clearing of forests, and introduction of exotic plant species, Iowa has lost most of its historical and natural prairies.

Here, we report on the status and behaviors of grassland small mammals existing in Camp Dodge, Iowa. Although Camp Dodge is one of the few places left in central Iowa containing relatively large intact pieces of grasslands, it is still affected by direct and indirect human interference. Pressure to clear and row-crop so much land for agricultural practices increases stress on native flora and fauna. Unless we pay attention to Iowa's rapidly diminishing natural habitats, the state's unique blend of flora and fauna will be lost forever.

Because the world is composed of landscapes, spatial mosaics are the focus of landscape ecology (Forman and Godron 1986; Weins et al., 1993). From an ecological perspective, landscape ecology offers a way to consider environmental heterogeneity or "patchiness" in spatially explicit terms (Weins et al., 1993). The effect of patchiness has become a major focus of ecology, including optimal foraging theory and behavioral ecology (Houston et al., 1988; Krebs and Houston 1989; Lima and Zollner 1996) and population and metapopulation structure (Gilpin and Hanski 1991). We use the landscape ecology approach to look at the behavioral ecology of small grassland mammals in a fragmented landscape.

Goals and Objectives

Two studies were conducted on Camp Dodge, Iowa. In the first study, we quantified spatial and temporal dynamics of grassland small mammals, looked at habitat associations, species' interactions, and described the effect of mowing on the abundance of small grassland mammals.

The second study focused on the effects of habitat heterogeneity and patchiness on the foraging and movement behaviors of the white-footed mouse (*Peromyscus leucopus*). An understanding on how very small patches of habitat may act as linking factors in an otherwise fragmented landscape is important to conservation and management decisions.

Thesis Organization

This thesis consists of a general introduction, one manuscript prepared for publication to *Proceedings of the Iowa Academy of Sciences*, one manuscript to be prepared for publication to *Oikos*, and a general conclusion. The first manuscript will be submitted as part of a symposium of researchers who have worked and conducted studies on Camp Dodge, IA. The two manuscripts will be submitted for publication under the authorship of Jessemine L. Fung, who conducted and summarized the research, and Brent J. Danielson, who provided supervision for the research and edited the manuscripts.

Literature Cited

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 23: 27-43.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9: 129-136.

Diffendorfer, J.E., M.S. Gaines, and R.D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon, Microtus,* and *Peromyscus*). *Ecology* 76: 827-839.

Forman, R.T.T. and M. Gordon. 1986. Landscape ecology. Wiley, New York.

Gilpin, M.E. and Hanski, I. 1991. *Metapopulation dynamics*. Academic Press, New York.

Houston, A., C. Clark, J. McNamara, andM. Mangel. 1988. Dynmamic models in behavioral and evolutionary ecology. *Nature* 332: 29-34.

Krebs, J.R. and A. Houston. 1989. Optimization in ecology. In: Cherrett, J.M. (ed.). *Ecological concepts*. Blackwell, Oxford. pp. 309-338.

Lima, S. and P. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131-135.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380.

CHAPTER 2. THE SPATIAL AND TEMPORAL DYNAMICS OF SMALL MAMMALS IN THREE DIFFERENT GRASSLAND HABITATS

A paper to be submitted to *Proceedings of the Iowa Academy of Sciences*

Jessemine L. Fung and Brent J. Danielson

Abstract

We investigated the spatial and temporal dynamics of grassland small mammals in Camp Dodge, Iowa, using the standardized methods of collecting and recording data for the U.S. Army Land Condition-Trend Analysis (LCTA) program. The six most commonly found species were prairie voles (*Microtus ochrogaster*), meadow voles (*Microtus pennsylvanicus*), prairie deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*), western harvest mice (*Reithrodontomys megalotis*), and the short-tailed shrew (*Blarina brevicauda*). We also found the rare least weasel (*Mustela nivalis*) in 1998, and the state-endangered plains pocket mouse (*Perognathus flavescens*) in 1999. A negative relationship between *M. ochrogaster* and *M. pennsylvanicus* was found. The deer mouse, *P. maniculatus* was found most often in the native grasses areas. A negative correlation between *P. maniculatus* and *R. megalotis* was also found. The annual fire regime in Camp Dodge may contribute to the lack of litter, which may affect habitat selection by these two species. Mowing disturbances affected these grassland species, decreasing their numbers after the event. We suggest that a rotational mowing and burning schedule may be beneficial to the overall diversity of mammals on the Camp.

Introduction

Camp Dodge, a United Sates Army training site located in central Iowa, provides an opportunity for the Army to manage its land for both military and nonmilitary ends,

including fish and wildlife support, recreation, and agricultural purposes. The U.S. Army Construction Engineering Research Laboratory (USACERL) developed the U.S. Army Land Condition-Trend Analysis (LCTA) program, which uses standard methods to collect and synthesize natural resources data on military training grounds throughout the nation. Development of the LCTA program has been driven by four major factors: 1) the Army's land-management challenge, 2) the need for sufficient training land, 3) recommendations of natural-resource experts, and 4) environmental compliance requirements (Tazik et al., 1992). Because the Army has been presented with the challenge of proper land management, we were provided with an opportunity to examine the spatial and temporal dynamics of grassland small mammals under the auspices of the LCTA program. The main objective of this study is to quantify the degree to which densities of small mammals vary among large regions of contiguous grassland on the Camp.

A previous survey of small mammals in similar habitats found little or no difference in the small mammals captured in prairie, old-field, and replanted monoculture habitats (Hayslett and Danielson 1994). However, their samples were taken from small plots (0.8 to 16.2 ha.) in Jasper and Polk counties and, thus, may reflect the effects of nearby habitats rather than the sampled patches. At Camp Dodge, individual patches of single types of habitat are much larger (20 to 50 ha.), thereby reducing the possibility of the samples being confounded by immigration from nearby patches of different qualities (i.e., rescue effects, Brown and Kodric-Brown 1977).

Habitat preference influences the distribution and abundance of small mammals. Some small mammals have specific habitat requirements and limited distributions, while others occupy a variety of habitats (Kaufman and Fleharty 1974). The data we describe here

can provide good estimates of the small-mammal diversity of Camp Dodge by habitat type. The data also allow us to locate areas within the Camp that currently have species of special concern. While these data are valuable in determining small-mammal distributions and abundances, they are not necessarily indicative of habitat quality or preference (Van Horne 1983, Pulliam 1988). Habitat quality should be defined in terms of the survival and reproduction characteristics, as well as density of the species occupying that habitat (Van Horne 1983).

The surveys also can be used to examine long-term trends in the abundances and species richness. This will allow Camp managers to determine whether particular species are being maintained or slowly lost in the grassland community. In a previous study by Schwartz and Whitson (1987), they hypothesized that these reconstructed sites were sub-optimal habitat for common prairie mammals due to low forb abundance and relatively homogeneous vegetation structure. Habitats containing native grasses on Camp Dodge were replanted monocultures of big bluestem (*Andropogon gerardi*) and Indian grass (*Sorghastrum nutans*), resulting in very little vegetative structure or variation.

Temporal environmental fluctuations can affect populations (Hutchinson 1961, Wiens 1977, Huston 1979, Ricklefs 1987, Chesson and Huntly 1997). Two years of surveying allow us to detect fluctuating populations that may be due to temporary local phenomena such as the location of predator dens and nests, local disease outbreaks, weather patterns, or other ecological phenomena. This method can give us a more accurate snapshot of the small-mammal community in the camp. Lastly, we compare the effect of agricultural disturbance (mowing) on the small mammal community. Disturbances affecting preferred habitat might be more costly for some species than others (Geier and Best 1980). If vegetation is changed

and habitat is altered, populations of some species may benefit while others are affected adversely.

Small mammal habitat preferences

Some of the common grassland small mammals we anticipated finding were the prairie voles (*Microtus ochrogaster*), meadow voles (*Microtus pennsylvanicus*), prairie deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*), and western harvest mice (*Reithrodontomys megalotis*). Of the shrews, the short-tailed shrew (*Blarina brevicauda*) was the most common.

Both *M. ochrogaster* and *M. pennsylvanicus* have been found to occupy similar habitats of dense, grassy vegetation (Bailey 1924; Martin 1956; Getz 1961, 1970), which may provide suitable cover for runways and nesting sites (Hall 1955; Martin 1960). The diets of both species are also similar, consisting primarily of leaves and stems of herbaceous vegetation (Hatt 1930; Zimmerman 1965; Meserve and Klatt 1985). Dicotyledonous plants are generally preferred over monocotyledonous plants (Thompson 1965; Cole and Batzli 1979; Lindroth and Batzli 1984). However, Cole and Batzli (1979) and Lindroth and Batzli (1984) suggest that *M. ochrogaster* may consume a greater proportion of dicots than *M. pennsylvanicus*.

P. maniculatus has been found in open grassy areas ranging from sparse, short vegetation (Bee et al., 1981) to tallgrass habitats (Martin 1960; Kaufman and Fleharty 1974). The deer mouse, usually described as granivorous, eats seeds and nuts but has been known to eat fruits and insects as well (Bee et al. 1981).

Unlike the deer mouse, *P. leucopus* prefers areas with woody vegetation and is most abundant in densely wooded areas (Burt 1940; Gunderson 1950; Getz 1961; Kaufman and

Fleharty 1974; Manson et al., 1999). They have also been found in some tallgrass areas typical of riparian habitats where woody vegetation exists (Hall 1955; Jones 1964; Fleharty and Stadel 1968; Geier and Best 1980). The white-footed mouse is a good climber and spends much of its time in trees. The mouse's nest is sometimes placed among dense branches of trees or in abandoned bird or squirrel nests. Others are placed in hollow trees, under logs or in burrows. Its diet consists of grasses, seeds, nuts, and some insects.

The western harvest mouse, *R. megalotis*, inhabits a wide variety of habitats (Kaufman and Fleharty 1974; Bee et al., 1981), from relatively dry grasslands and dense weedy fields to brushy riparian areas. This species has been known to use below-litter runways made by other small mammals (Pearson 1959, Bee et al. 1981). This mouse eats seeds, green plant parts, and some insects.

The short-tailed shrew, *B. brevicauda*, is the largest shrew found in Iowa. It prefers the damp soils of grasslands and riparian communities (Geier and Best 1980; Bee et al., 1981). The shrew is semi-fossorial, using trails and burrows made by other small mammals. Their high metabolism and continuing need for food force them to eat insects and other small mammals; specialized teeth and poisonous saliva help immobilize and kill mouse-sized prey in 3 to 5 minutes after the bite is administered.

The small mammal community of central Iowa grasslands can be divided into three major trophic guilds: herbivores, granivores and omnivores, and carnivores. Of these three, only the first two were well enough represented in this study to allow trophic-level analyses across habitat types.

Objectives

The objectives of this study are to 1) quantify a baseline for species richness and abundance in Camp Dodge that can be used as a basis of comparison for subsequent surveys for the purpose of identifying long-term trends in the grassland small mammal community; 2) assess species richness and abundance in replanted native grasses, old-field grasslands dominated by cool season grasses, and the cultivated hayfields; and 3) assess how mowing in the alfalfa (*Medicago sativa*) and old-field grasslands affects species richness and abundance.

Methods

Study area

This area differs from the rest of central Iowa in that grassland cover is extensive in the Camp. Several types of grassland habitats exist in the Camp. The first and predominant habitat is composed of nonnative grasses typical of old-fields composed of grasses such as brome (*Bromus inermis*) and bluegrass (*Poa pratensis*). The second habitat type is represented by the extensive plantings of native grasses, mostly big bluestem (*Andropogon gerardi*) and Indian grass (*Sorghastrum avenaceum*). These warm-season grasslands contained very few forbs of any type. The third habitat type is cultivated alfalfa (*Medicago sativa*) fields—again, with very few other species of plants.

Site selection and sampling methodology

Sampling transects were predetermined by the LCTA program. The LCTA permanent transects are 100 x 6 m with a 100-m line transect forming the longitudinal axis. Transect locations were randomly selected from an array of all land-cover and soil categories established by incorporating SPOT (Système Probatoire pour l'Observation de la Terre)

satellite imagery, digital soil surveys, and Geographic Resources Analysis Support System (GRASS) geographic information system (Tazik et al. 1992). The number of transects assigned to each category was proportional to the land area in each category. In the case of Camp Dodge, 30 transects were established in areas ranging from woodlands to cultivated alfalfa fields. Of the 30, we sampled 23 transects that were located in the grasslands. Three transects were located in native grasses habitat, twelve in nonnative grasses habitat, and eight in the alfalfa fields.

During the first year (1998), we sampled during three periods: mid-spring (mid May), mid-summer (early July), and mid-autumn (late October). For the second year (1999), we sampled only during the first two periods. Based on the previous year's experience, we felt that the third sampling session after the fields were mowed did not contribute significantly to our data.

At each transect, 11 trapping stations were spaced at 10-m intervals. At each station, two 8 x 9 x 23 cm standard Sherman live traps (H.B. Sherman Traps, Inc. Tallahassee, FL.) were placed approximately 0.5 m on either side of the transect. The traps were baited with whole oats and locked open for two nights. Immediately after this interval, we set the traps for capture on 5 successive nights, checking them each morning. Captured mammals were identified to species, marked with ear tags, weighed, sexed, and immediately released.

Results

Eleven species of small mammals were captured in 1998 during 7590 trap nights while 12 species were captured during 6050 trap nights in 1999. The six most common small mammals found were prairie voles (*Microtus ochrogaster*), meadow voles (*Microtus*

pennsylvanicus), prairie deer mice (*Peromyscus maniculatus*), white-footed mice (*Peromyscus leucopus*), western harvest mice (*Reithrodontomys megalotis*), and short-tailed shrews (*Blarina brevicauda*) (Table 1). With the exception of *P. maniculatus*, approximately twice as many of each of the six species were captured in 1998 than 1999 (Table 1 and Fig. 1). In addition, Fig. 1 shows the seasonal differences in the number of individual captures for both 1998 and 1999, and illustrates how many more individuals of each species were found in 1998 than in 1999. Two species of special concern to Camp personnel were found in both years: the least weasel (*Mustela nivalis*) in 1998, and the plains pocket mouse (*Perognathus flavescens*) in 1999. Although not federally threatened species, both are rare in Iowa (*P. flavescens* is an Iowa Threatened and Endangered Species; Bowles 1998).

Other species captured were the house mouse (*Mus musculus*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), eastern chipmunk (*Tamias striatus*), eastern cottontail rabbit (*Sylvilagus floridanus*), and prairie jumping mouse (*Zapus hudsonicus*). Due to the reduction in numbers of species after mowing, we did not survey during the late season trapping session in 1999.

Species richness did not differ markedly among the three habitat types in either 1998 or 1999 (Table 2). The distributions of the six most commonly captured species in Camp Dodge for each habitat type for 1998 and 1999 are also given in Figure 2. In 1998, *M. ochrogaster* was the predominant species found in the nonnative habitat, while in 1999, *M. pennsylvanicus* dominated the same habitat. *P. maniculatus* was the dominant species found in the native habitat in 1999.

Because there were unequal numbers of transects in each habitat type (3 in native, 8 in alfalfa, and 12 in nonnative), we summarize captures using the mean minimum number

known alive (MNA) per transect in each habitat type. Standardized numbers of species abundance in each habitat type were categorized by trophic guilds (Figs. 3 and 5; mean standardized numbers of species abundance ± SE). As vegetative structure increased in complexity (from monocultures of alfalfa to the heterogeneous nonnative grasses), increasing numbers of herbivores were seen. While *M. ochrogaster* was the most numerous herbivore in the nonnative grassland habitats in 1998, *M. pennsylvanicus* was the most numerous herbivore in the same habitat type in 1999.

Because these two species are believed to be competitors (Zimmerman 1965; Steele 1977; Cole and Batzli 1979; Baker and Brooks 1982; Lindroth and Batzli 1984; Getz et al. 1987;), we tested our data for correlations between the two species. We selected all transects in which both species occurred and correlated the numbers of each species observed at each trap station (two traps per station) during each 5-day trapping period. This analysis provides insight into micro-scale interactions that could result from very subtle variation in habitat along each transect. We found a negative correlation between these two species ($p < 0.01$, 1998; $p < 0.01$, 1999; Spearman correlation; Fig. 4). However, neither regression explains a high amount of the variance ($r^2 = 0.167$, 1998; $r^2 = 0.353$, 1999).

More complicated relationships were found among the granivores (Fig. 5). Because *P. maniculatus* and *R. megalotis* have been known to associate together in grassy habitats, we tested our data for correlations between the two species. Again, we selected all transects in which both species occurred and correlated the numbers of each species observed at each trap station during each 5-day trapping period. There was a negative correlation between these two species in habitats where they were found ($p < 0.01$, 1998; $p < 0.01$, 1999; Spearman

correlation; Fig. 6). Although there was a significant negative correlation between these two species, native grasslands were the preferred habitat for *P. maniculatus* (Fig. 5).

P. leucopus generally prefer riparian habitats containing woody vegetation (Kaufman and Fleharty 1974; M'Closkey and Feldwick 1975; Geier and Best 1980; Manson and Stiles 1998). Thus, they were not commonly found in the grassland habitats we surveyed.

The autumn trapping period showed a marked decline in all species. This could be a seasonal effect. However, most of the fields were mowed shortly before this trapping period, and thus mowing may have been the primary cause of this reduction. Of the 23 transects, 18 were mowed by the autumn trapping period. We compared the average number of each species in these transects to the average number in the remaining 5 unmowed transects (Fig. 7; mean standardized number of species abundance ± SE). All species except *M. ochrogaster* were at lower densities in the mowed areas suggesting that mowing is responsible for at least a substantial proportion of the autumn decline.

Discussion

Yearly species richness was similar in the areas we trapped in Camp Dodge. Species abundances, however, differed markedly with a twofold decrease in 1999. Seasonal and annual population differences may be due to environmental fluctuations and corresponding shifts in the intensity of competition within and between the species.

We found interesting patterns of habitat preference when we grouped the common grassland species into trophic guilds. The herbivores, *M. ochrogaster* and *M. pennsylvanicus*, were the most abundant small mammals. For unknown reasons, the two species showed dramatically different densities in the native and nonnative grass habitats in

1998. However, when densities were much lower in 1999, this dichotomy did not exist (Fig. 3). This suggests that these habitats may not be as desirable as alfalfa and are used only when high densities push animals into lower preference habitats (Rosenzweig 1981, Morris 1988; Morris 1996).

At the smallest scale (single trap stations) we found a negative relationship between these two species, suggesting interspecific competition is occurring. Getz et al. (1987) and Zimmerman (1965) found a similar negative association between the two species in Illinois and Indiana. Getz et al. (1987) attributed the relationship to different strategies used by the two species to reduce predation risk. The preference of *M. ochrogaster* for dense vegetation is not as great as the preference exhibited by *M. pennsylvanicus* (Zimmerman 1965; Steele 1977; Baker and Brooks 1982; Getz et al., 1987). In addition, *M. pennsylvanicus* nests primarily on the surface of the ground or even slightly above ground in clumps of vegetation (Hatt 1930; Jackson 1961) while *M. ochrogaster* nests most frequently in elaborate burrow systems (Wolff 1985). The underground nesting habit of *M. ochrogaster* may provide them with sufficient protection from predators in areas of sparse vegetation analogous to the vegetative cover providing protection to *M. pennsylvanicus*.

The high numbers of *P. maniculatus* that we observed in native-grass habitat agrees with other studies (Jones 1964; Andersen and Fleharty 1967; Kaufman and Fleharty 1974; Geier and Best 1980). Preference of this species for tall grasses is probably related to the amount of cover and food provided by such habitats (Jones 1964; Andersen and Fleharty 1967). Because the *P. leucopus* prefer areas of high structural complexity, such as shrubs (M'Closkey and Feldwick 1975; Geier and Best 1980; Bowers and Dooley 1993; Manson and Stiles 1998; Manson et al., 1999), they were seldom found in the relatively low structural

diversity of the replanted native grass habitats and alfalfa fields. Contrary to some studies that found *R. megalotis* and *P. maniculatus* to have moderate to high habitat breadth across a variety of habitats (Kaufman et. al, 1990; Hayslett and Danielson 1994), we found them to prefer the replanted native grasses. Habitat selection by *P. maniculatus* and *R. megalotis* differs according to the amount of litter found on the ground. Kaufman et al., (1988) found that the lack of litter was the most important feature that resulted in a positive response by *P. maniculatus* to conditions following a fire. Competition between the larger granivore, *P. maniculatus* (*P. maniculatus*, 18.5-25 g; *R. megalotis* 11.6-16 g; Bee et al., 1981), may also play a role in the lower densities of *R. megalotis* in the same habitat (Kaufman et al., 1988).

Due to the mowing disturbance in late July and August of 1998, we saw a decrease in the abundance of species (Fig. 7). Loss of food and cover provided by the vegetation was probably the cause of the reduction. Harsh conditions can reduce population growth rates, and they may reduce the intensity of interactions between species. However, unless fluctuations in environmental conditions (e.g., disturbance, seasonal change, and weather variation) create unique spatial or temporal niche opportunities, coexistence among species will not be promoted (Chesson and Huntly 1997). As Geier and Best (1980) predicted, grass removal did affect grassland small mammals negatively.

Two rare species were found on the camp: the least weasel, *Mustela nivalis*, in alfalfa and nonnative grass fields in 1998, and the plains pocket mouse, *Perognathus flavescens*, in a dry and sandy nonnative grass habitat. *M. nivalis* is the smallest member of the order Carnivora in Iowa and appears restricted to the northern portion of the state (Bowles 1998). Their occurrence in Camp Dodge is indicative of a species at the edge of its geographic range.

P. flavescens is a state endangered species primarily occupying the western grasslands of the state (Bowles 1998). Thus their occurrence here is also symptomatic of a species on the edge of its range. They prefer dry areas of sandy soils where vegetation is sparse (Bee et al. 1981). Like gophers, the plains pocket mouse will plug the main entrance to its burrow during daylight. This may be the reason that that their denning areas are characterized by many small holes localized in sandy and soft soils (hard clay soils being too difficult for frequent burrowing). Such soils are rare on Camp Dodge and may need to be carefully managed and protected if this species is to be retained on the site. The mice feed exclusively on grass seeds and may be compete with *P. maniculatus* or *R. megalotis*.

Camp Dodge provided us an opportunity to survey large areas of grassland that are becoming rare in central Iowa. As a result, we found the species typical of grasslands as well as a few rare species. As pressure to clear and row-crop as much land as possible continues in Iowa, increasing stress will be placed on the native flora and fauna. To maintain the diversity of small mammals on Camp Dodge over the long-term, we recommend that mowing disturbances be managed carefully. Perhaps creating a rotational mowing regime that allows unmowed habitat near each mowed field will maximize the opportunities for mammals to quickly recolonize mowed areas as the vegetation recovers.

The recent shift to native grasses in pastures and fields may have created additional habitat for some grassland mammals. However, emphasis on creating vegetative diversity instead of monoculture stands of native grasses should be considered as it may increase the diversity and coexistence of species. Also, the rigorous annual burning, while beneficial to some species such as *P. maniculatus*, may be detrimental to other species such as *B. brevicauda*, which were in lower abundances that we anticipated. We suggest that a

rotational burning schedule may be beneficial to the overall diversity of mammals on the Camp.

Literature Cited

Andersen, K.W., and E.D. Fleharty. 1967. Mammalian distribution within biotic communities of northeastern Jewell County, Kansas. Fort Hays Studies, Scientific Serial 6: 46 pp.

Bailey, V. 1924. Breeding, feeding, and other life habits of meadow mice (*Microtus*). J. Ag. Res. 27: 523-535.

Baker J.A., and R.J. Brooks. 1982. Impact of raptor predation on a declining vole population. *J. of Mamm.* 63: 297-300.

Bee, J.W., G. Glass, R.S. Hoffmann, and R.P. Patterson. 1981. Mammals of Kansas. University of Kansas, Museum of Natural History. pp. 300.

Bowers, M.A., and J.D. Dooley. Jr. 1991. Landscape composition and the intensity and outcome of two-species competition. Oikos 60: 180-186.

Bowles, J.B. 1981. Iowa's mammal fauna: An era of decline. Proc. Iowa Acad. Sci. 88: 38-42.

——. 1998. Mammals of Iowa: Holocene to the end of the 20th century. 1998. Proc. Iowa Acad. Sci. 105:123-132.

Brown, J.H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecol. 58: 445-449.

Burt, W.H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ., University of Michigan Museum of Zoology 45: 1-58.

Cole, F.R., and G.O. Batzli. 1979. Nutrition and population dynamics of prairie vole, *Microtus ochrogaster*, in central Illinois. J. An. Ecol. 48: 455-470.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat. 150:519-553.

Fleharty, E.D., and D.L. Stadel. 1968. Distribution of *Peromyscus leucopus* (Woods Mouse) in western Kansas. Trans. Kansas Acad. Sci. 71: 231-233.

Geier, L.L., and L.B. Best. 1980. Habitat selection by small mammals of riparian communities: Evaluating effets of habitat alteration. J. Wildl. Manage. 44: 16-24.

Getz, L.L. 1961. Factors influencing the local distribution of *Microtus* and *Synaptomys* in southern Michigan. Ecol. 42: 110-119.

——. 1970. Influence of vegetation on the local distribution of the meadow vole in southern Wisconsin. University of Connecticut Occas. Pap. 1: 213-241.

Getz, L.L., J.E. Hofman, B.J. Klatt, L. Verner, F.R. Cole, and R.L. Lindroth. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *Microtus pennsylvanicus* in east central Illinois. Can. J. Zool. 65: 1317-1325.

Gunderson, J.L. 1950. A study of some small mammal populations at Cedar Creek Forest, Anoka County, Minnesota. University of Minnesota Press, Minneapolis, pp. 49.

Hall, E.R. 1955. Handbook of mammals of Kansas. Misc. Publ., University of Kansas Museum of Natural History 7: 1-303.

Hatt, R.T. 1930. The biology of the voles of New York. Roosevelt Wildlife Bulletin 5: 513-623.

Hayslett, L.A., and B.J. Danielson. 1994. Small mammal diversity and abundances in three central Iowa grassland habitat types. Prairie Nat. 26: 37- 44.

Jackson, H.H.T. 1961. Mammals of Wisconsin. University of Wisconsin Press, Madison, pp. 504.

Jones, J.K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Publ., Museum of Natural History 16: 1-365.

Kaufman, D.W., B.K. Clark, and G.A. Kaufman. 1990. Habitat breadth of nongame rodents in the mixed-grass prairie region of north central Kansas. Prairie Nat. 22: 19-26.

Kaufman, D.W., and E.D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwest Nat. 18: 443-452.

Kaufman, G.A., D.W. Kaufman, and E.J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. 1988. J. Mamm. 69:342-352.

Lindroth, R.L., and G.O. Batzli. 1984. Food habits of the meadow vole (*Microtus pennsylvanicus*) in bluegrass and prairie habitats. J. Mamm. 65: 600-606.

Manson, R.H., and E.W. Stiles. 1998. Links between microhabitat preferences and seed predation by small mammals in old-fields. Oikos 82: 37-50.

Manson, R.H., R.S. Ostfeld, and C.D. Canham. 1999. Responses of a small mammal community to heterogeneity along forest-old-field edges. Land. Ecol. 14: 355-367.

Martin, E.P. 1956. A population study of the prairie vole (*Microtus ochrogaster*) in northeastern Kansas. University of Kansas Publication, Museum of Natural History 8: 316-416.

——. 1960. Distribution of native mammals among the communities of mixed prairie. Fort Hays Studies, Scientific Serial 1: 1-26.

M'Closkey, R.T., and B. Feldwick. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). J. Mamm. 56: 119-129.

Meserve, P.L., and B.J. Klatt. 1985. Evidence of noncycling populations and the importance of immigration in voles inhabiting an Illinois tallgrass prairie. Am. Midl. Nat. 113: 255-270.

Morris, D.W. 1988. Habitat-dependent population regulation and community structure. Evol. Ecol. 2:253-269.

——. 1996. Temporal and spatial population dynamics among patches connected by habitat selection. Oikos 75:207-219.

Palmer, M.W. 1988. The coexistence of species in fractal landscapes. Am. Nat. 139: 375-397.

Pearson, O. P. 1959. A traffic survey of *Microtus - Reithrodontomys* runways. J. Mamm. 40: 169-180

Rosenzweig, M.L. 1981. A theory of habitat selection. Ecol. 62:327-335.

Schwartz, O.A., and P.D. Whitson. 1987. A 12-year study of vegetation and mammal succession on a reconstructed tallgrass prairie in Iowa. Am. Midl. Nat. 117: 240-249.

Steele, R.W. 1977. A demographic study of *Microtus pennsylvanicus* in relation to habitat structure. Unpubl. M.S. thesis; University of Guelph, Ontario, Canada.

Tazik, D.J., S.D. Warren, V.E. Diersing, R.B. Shaw, R.J. Brozka, C.F. Bagley, and W.R. Whitworth. 1992. U.S. army land condition-trend analysis (LCTA) plot inventory field methods. In USACERL Technical Report N-92/03.

Thompson, D.Q. 1965. Food preferences of meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. Am. Midl. Nat. 74: 76-86.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893-901.

Wolff, J.O. 1985. Behavior. *In* Biology of New World *Microtus* (R.H. Tamarin, ed.,). pp 340-372. Special Publication No. 8, American Society of Mammalogists.

Zimmerman, E.G. 1965. A comparison of habitat and food of two species of *Microtus*. J. Mamm. 46: 605-612.

Table 1. The number of initial small mammal captures in Camp Dodge, in May, June, July, October 1998 and May and July 1999.

Species	Individual captures 1998	Individual captures 1999
Murid rodents		
Microtus ochrogaster	325	72
Microtus pennsylvanicus	122	65
Peromyscus maniculatus	96	63
Peromyscus leucopus	94	10
Reithrodontomys megalotis	94	42
Mus musculus	3	1
*Perognathus flavescens**	0	1
Zapus hudsonius	0	1
Shrews		
Blarina brevicauda	22	11
Sorex spp.	3	0
Small Weasels		
*Mustela nivalis**	2	0
Small ground squirrels		
Spermophilus tridecemlineatus	1	2
Other small mammals		
Tamias striatus	3	4
Sylvilagus floridanus	0	1

* species that are of special interest because they are rare and/or because their range boundaries occur in central Iowa. These species are not federally endangered or threatened; instead they are listed by the Iowa Department of Natural Resources to be of special concern in Iowa.

Table 2. The number of individuals of each species found in each habitat type in Camp Dodge, Iowa in 1998 and 1999.

Species	Alfalfa			Native grasses			Nonnative grasses		
	1998	1999	Total	1998	1999	Total	1998	1999	Total
Murid rodents									
Microtus ochrogaster	54	30	94	58	11	69	233	31	264
Microtus pennsylvanicus	48	10	58	20	3	23	74	52	126
Peromyscus maniculatus	27	10	37	32	43	75	38	10	48
Peromyscus leucopus	6	0	6	1	1	2	87	10	97
Reithrodontomys megalotis	16	14	30	39	1	40	39	27	66
Mus musculus	2	1	3	1	0	1	0	0	0
*Perognathus flavescens**	0	0	0	0	0	0	0	1	0
Zapus hudsonius	0	0	0	0	0	0	0	1	1
Shrews									
Blarina brevicauda	3	6	9	1	0	1	18	5	23
Sorex spp.	2	0	2	0	0	0	1	0	1
Small Weasels									
*Mustela nivalis**	1	0	1	0	0	0	1	0	1
Small ground squirrels									
Spermophilus tridecemlineatus	0	0	0	0	0	0	0	2	2
Other small mammals									
Tamias striatus	0	0	0	0	0	0	3	4	7
Sylvilagus floridanus	0	0	0	0	0	0	0	1	1

* species that are of special interest because they are rare and/or because their range boundaries occur in central Iowa. These species are not federally endangered or threatened; instead they are listed by the Iowa Department of Natural Resources to be of special concern in Iowa.

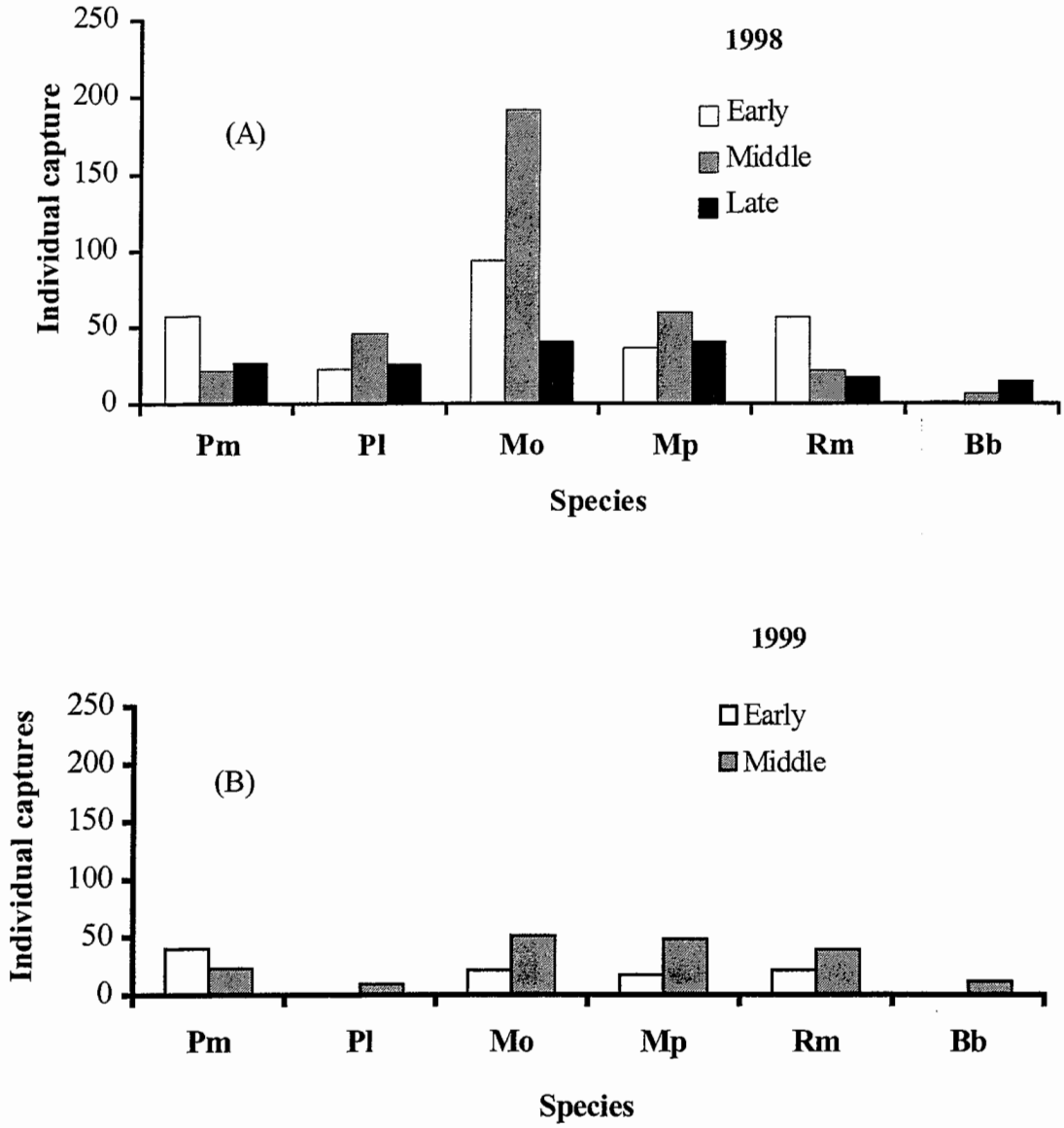


Fig. 1. Unique, individual captures of the six most commonly found small mammal species during the Early (mid May), Middle (early July), and Late (late October) trapping sessions. (A) 1998 season captures during each of the three trap sessions. (B) 1999 season captures, scaled to the 1998 numbers for comparison. Only two trapping sessions were conducted during the 1999 season. Pm=*P. maniculatus*, Pl=*P. leucopus*, Mo=*M. ochrogaster*, Mp=*M. pennsylvanicus*, Rm=*R. megalotis*, Bb=*B. brevicauda*.

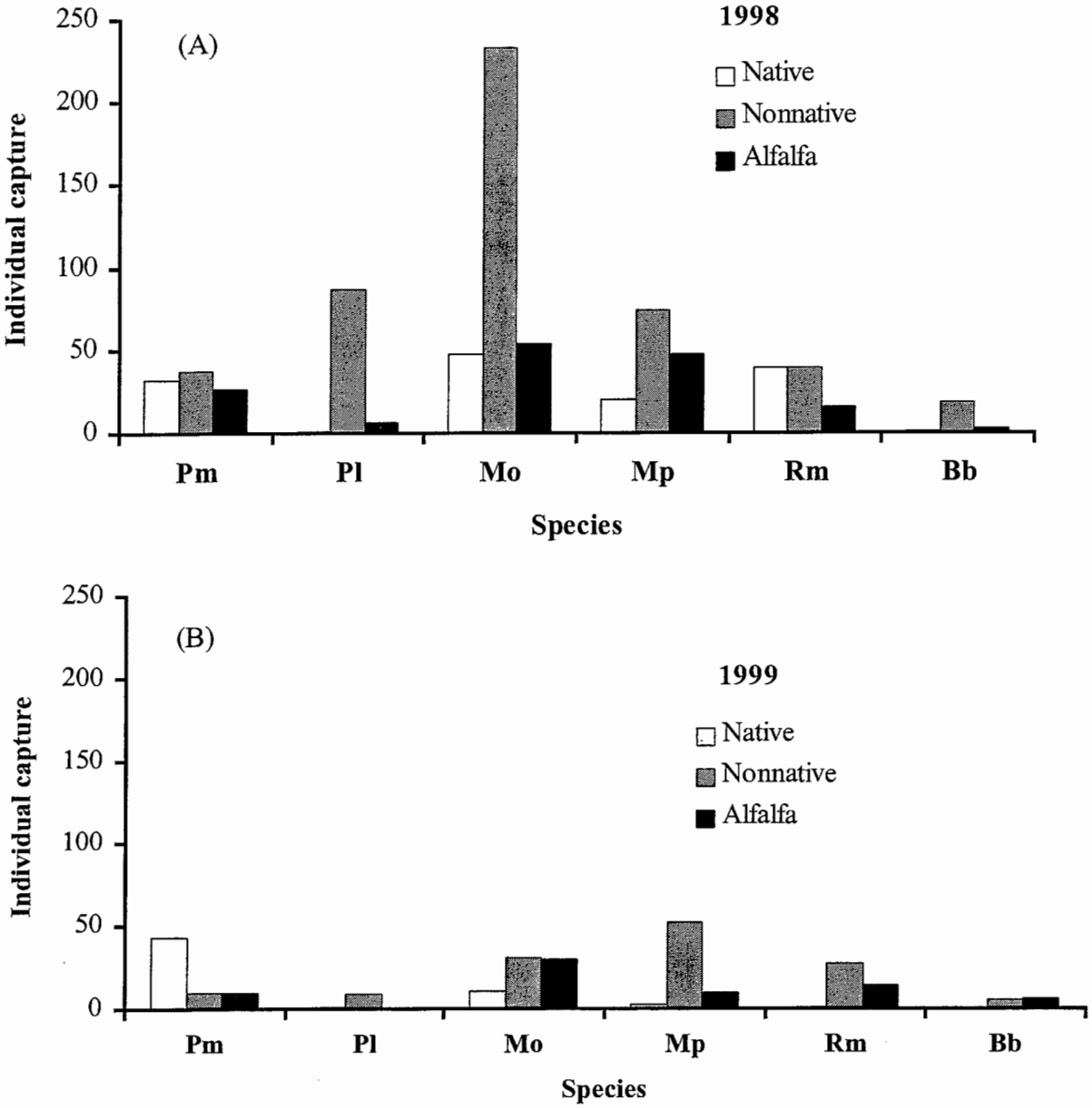


Fig. 2. The total number of individual captures of the six most commonly found small mammals for the (A) 1998 season and (B) 1999 season in each habitat type. The grassland habitats were divided into three distinct categories based on dominant vegetation: Native grasses, nonnative grasses, and alfalfa. For year to year comparison, the graphs were scaled similarly. Pm=*P. maniculatus*, Pl=*P. leucopus*, Mo=*M. ochrogaster*, Mp=*M. pennsylvanicus*, Rm=*R. megalotis*, Bb=*B. brevicauda*.

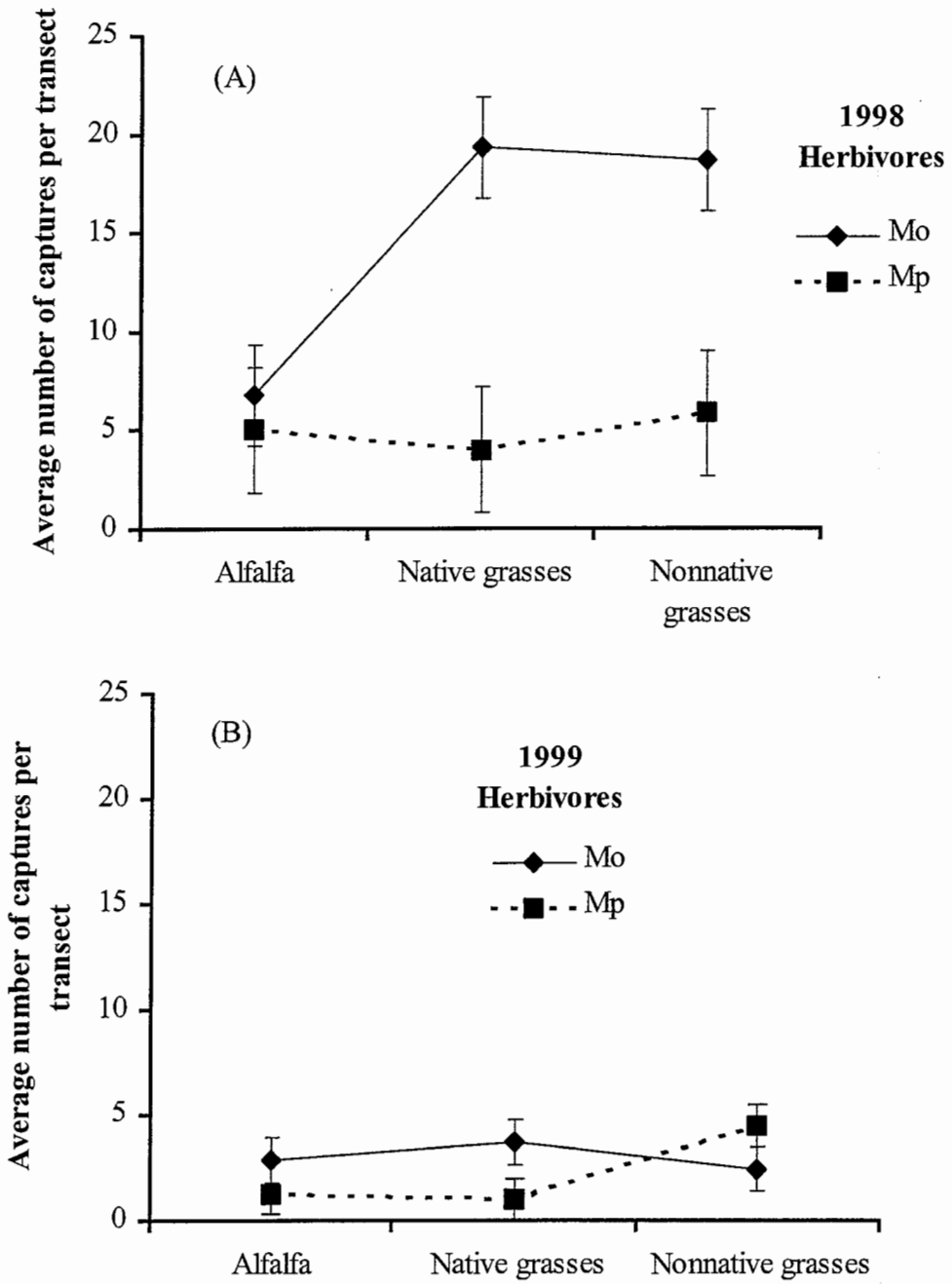
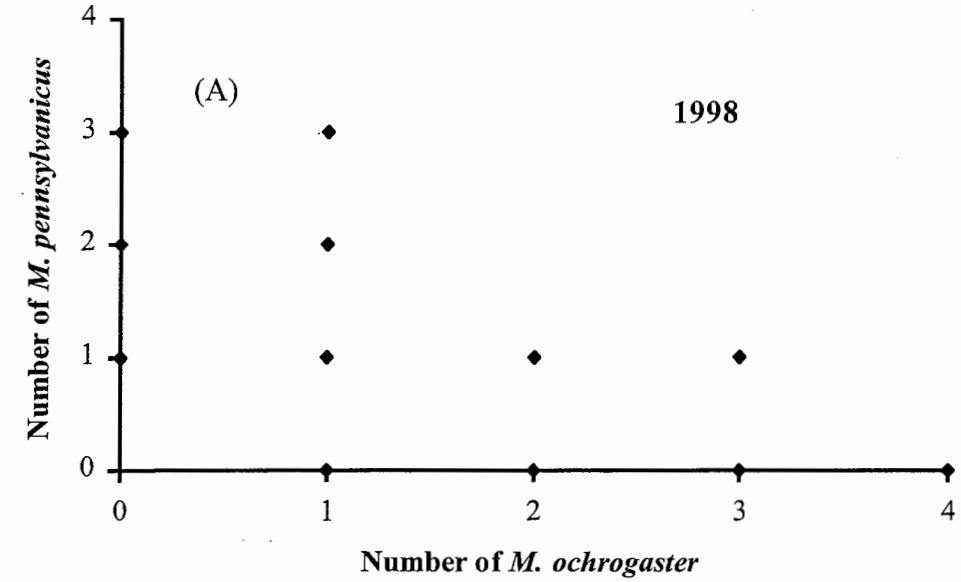


Fig. 3. Standardized numbers of individual hebivores in each of the three habitat types in (A) 1998 and (B) 1999 (mean ± SE). *M. ochrogaster* (Mo) and *M. pennsylvanicus* (Mp) were divided by the number of transects in each habitat type based on dominant vegetation (8 transects in alfalfa fields, 3 transects in native grasses, and 12 transects in nonnative grasses). Vegetative structure increased in complexity from alfalfa to old-field habitats.



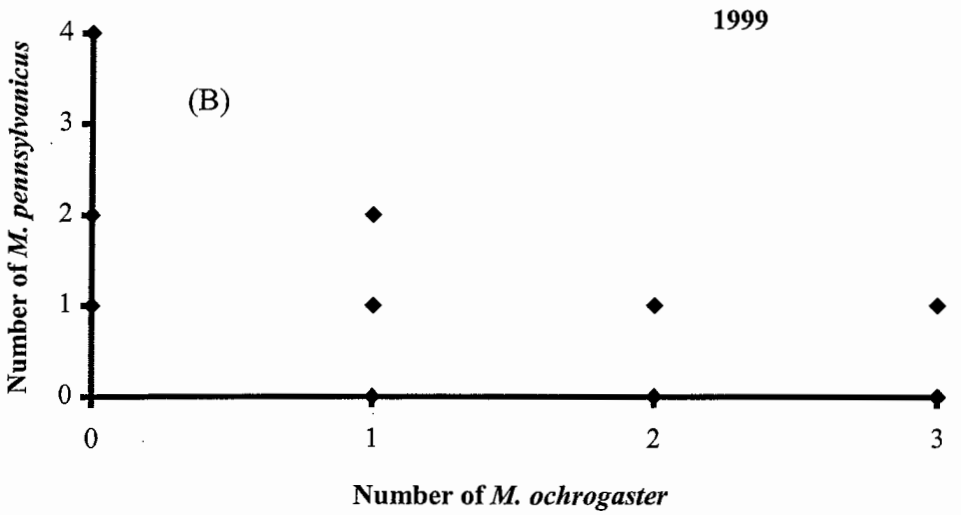
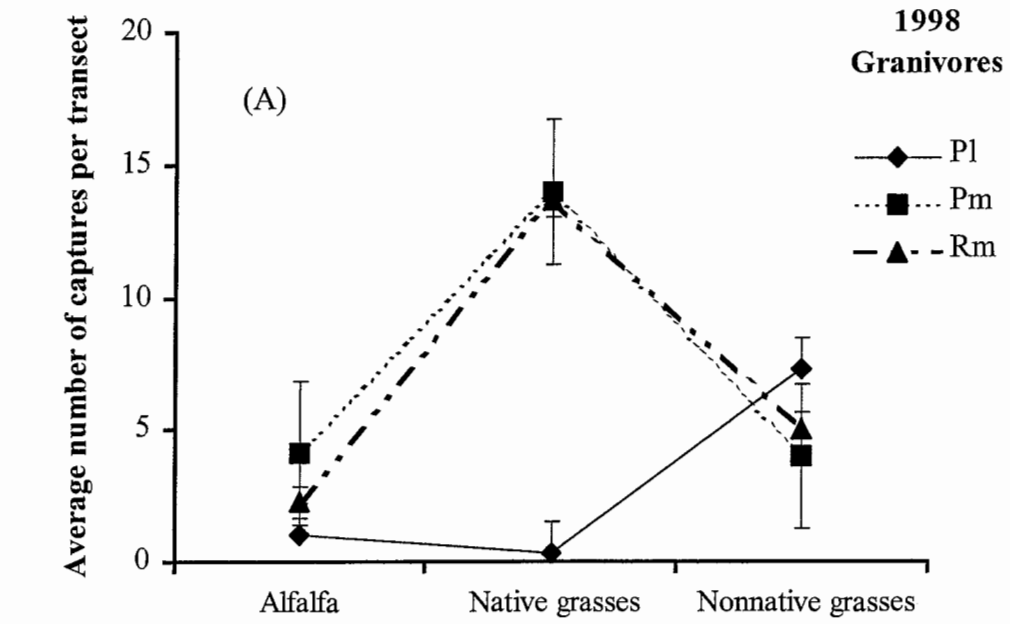


Figure 4. The minimum number alive (MNA) of *M. ochrogaster* (MIOC) and *M. pennsylvanicus* (MIPE) for each trap station of each transect where both species were found. (A) show the negative correlation in 1998 ($p < 0.01$, Spearman correlation), while (B) show the same trend in 1999 ($p < 0.01$, Spearman).



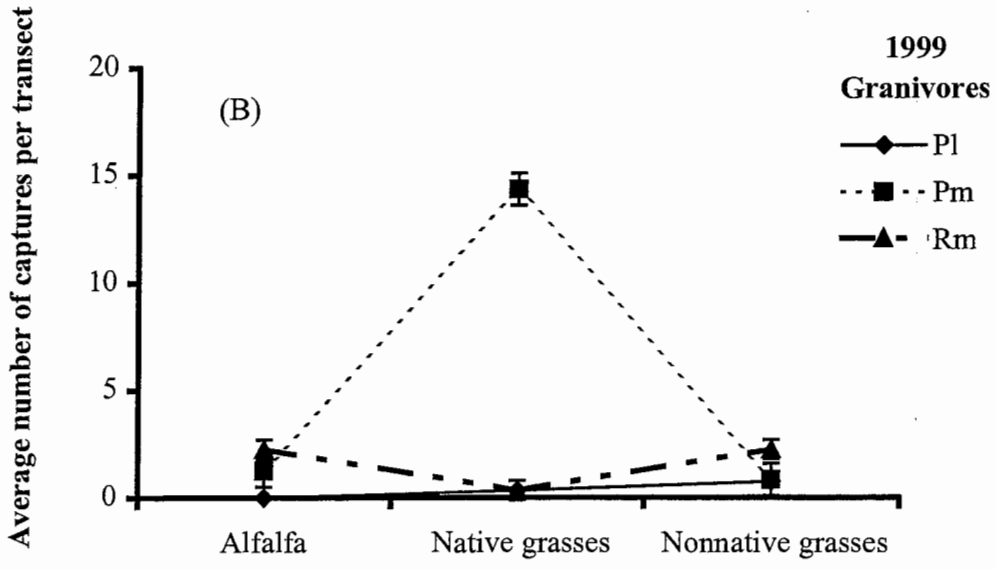


Figure 5. Standardized numbers of individual granivores in each of the three habitat types in (A) 1998 and (B) 1999. Individually captured *P. leucopus* (PELE), *P. maniculatus* (PEMA), and *R. megalotis* (RHME) were divided by the number of transects in each habitat type (8 transects in alfalfa fields, 3 transects in native grasses, and 12 transects in nonnative grasses habitat). Both graphs were similarly scaled for year to year comparison. We found fewer individuals in 1999 than in 1998.

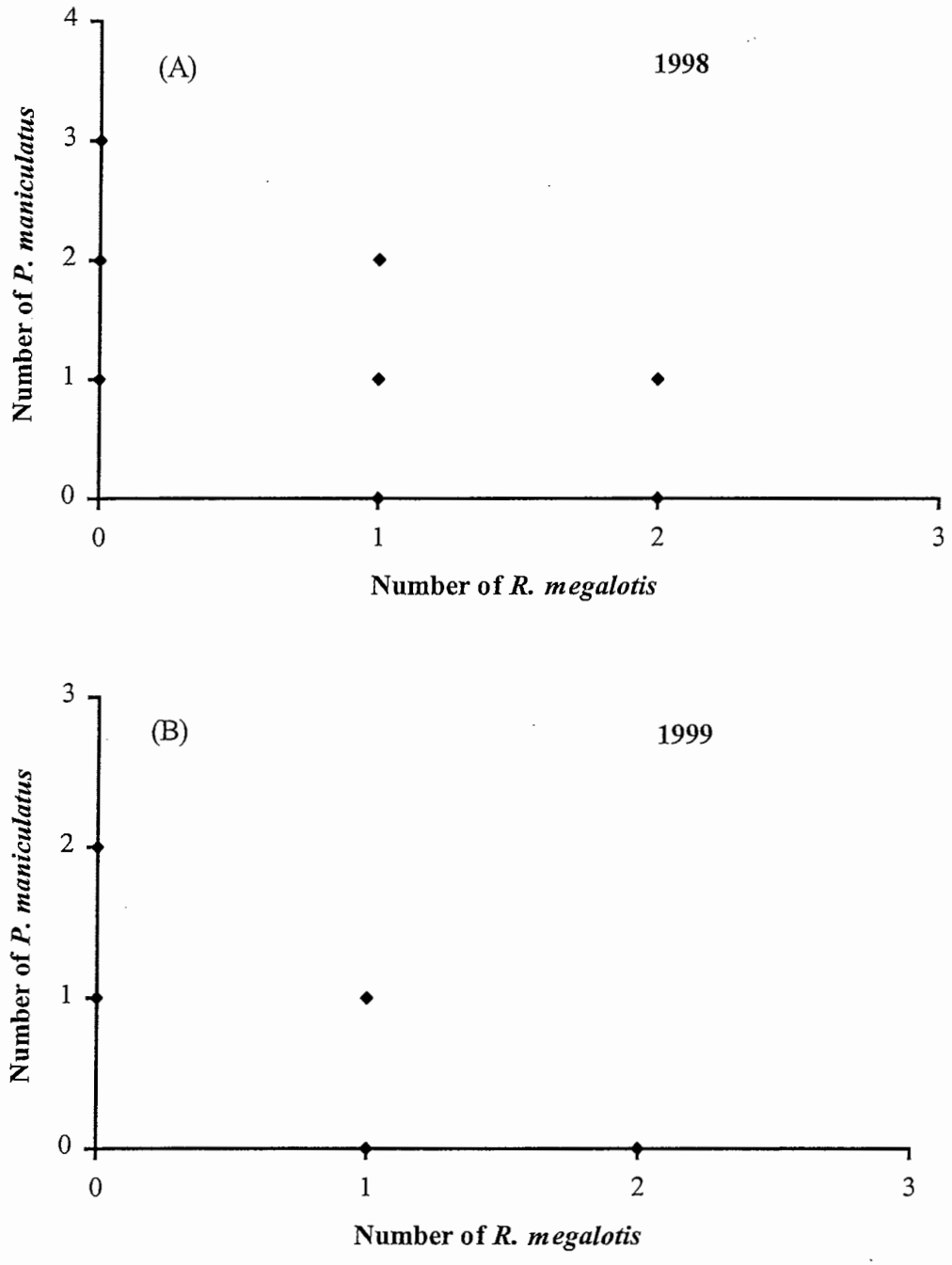


Figure 6. The minimum number alive (MNA) of *P. maniculatus* (PEMA) and *R. megalotis* (RHME) for each trap station of each transect where both species were found. (A) shows the negative correlation in 1998 ($p < 0.01$, Spearman correlation), while (B) shows the same trend in 1999 ($p < 0.01$, Spearman).

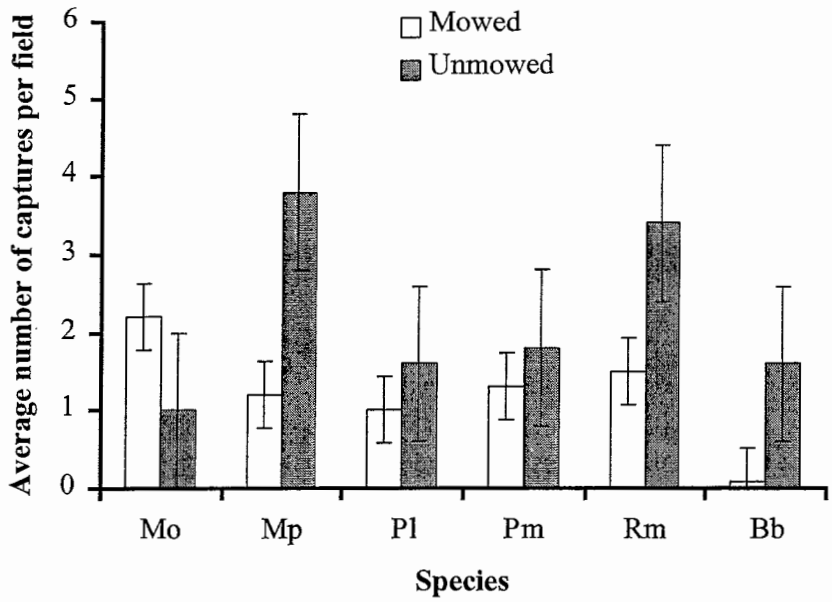


Figure 7. Although sample means were lower after mowing, only *M. ochrogaster* showed a significant difference (paired t-test, p = 0.05). The error bars are Standard Errors. Pm=*P. maniculatus*, Pl=*P. leucopus*, Mo=*M. ochrogaster*, Mp=*M. pennsylvanicus*, Rm=*R. megalotis*, Bb=*B. brevicauda*.

CHAPTER 3. RODENT OASES: MICROPATCHES AS LINKING FACTORS IN A FRAGMENTED LANDSCAPE

A paper to be submitted to *Oikos*.

Jessemine L. Fung and Brent J. Danielson

Abstract

Using live-trapping and giving-up densities (GUDs), we tested whether the use of micropatches (very small patches of habitat) influenced the use of large patches in a fragmented landscape. The white-footed mouse (*Peromyscus leucopus*) viewed micropatches as supplements to the surrounding patches and foraged in the micropatches. Further, we found that the mice moved between multiple patches of habitat more often in the presence of micropatches. Although our trapping data suggest that micropatches may promote *P. leucopus* movement in a fragmented landscape, our GUDs study showed that they may not forage equally in this landscape. The GUDs also show that in this particular study area, both the large patches and micropatches are identically-valued habitats. Micropatches that are very much smaller than the home range of a single individual may be important in evaluating the general quality of a fragmented landscape for supporting a population that predominantly resides in the larger fragments. There may be no patch of habitat that is so small as to be valueless to the welfare of the population.

Introduction

Traditionally, the study of landscapes has viewed the environment as composed of a set of isolated patches of habitat superimposed against a sea of uninhabitable matrix (MacArthur and Wilson 1967, Pickett and White 1985, Stephens and Krebs 1986, Shorrocks and Swingland 1990, Gilpin and Hanski 1991). However, understanding the relationships between these patches, rather than studying individual patches as discrete universes is key (Dunning et al. 1992). The goal of this study is to assess the effects of the spatial arrangement of different patches on the ability of white-footed mice (*Peromyscus leucopus*) to use the resources within patches in a fragmented landscape.

Fragmentation is the subdivision of a continuous habitat into many patches. Modeling of fragmented landscapes is often done using patch-based algorithms to study the relationship between landscape structure and population dynamics (Pickett and White 1985; Stephens and Krebs 1986; Shorrocks and Swingland 1990; Gilpin and Hanski 1991). These models are simplistic in their portrayal of landscapes; this is a holdover from the island biogeography theory (*sensu* MacArthur and Wilson 1967). While simplification is useful for intuiting the mechanisms behind ecological processes, landscapes are seldom binary mosaics.

Landscapes generally contain a variety of habitat types that may be used for different functions (reproduction vs. foraging), or to different degrees, based on habitat quality (e.g., Andrén 1990, Cummings and Vessey 1994). The key to understanding how landscape patterns affect populations is not only to concentrate on landscape physiognomy and composition, but also to recognize that there are a variety of habitat types. Many have done so using methods of fractal geometry to create neutral models with habitat distributions that

are more similar to actual landscapes than simple random maps (Milne 1992, Palmer 1992, With 1994, Wiens 1995, With and Crist 1995, With 1997). In addition, Danielson (1992) points out that incorporating the matrix into source-sink models can have a profound effect on a single-species' population. By explicitly considering the matrix, we may increase our understanding of the overall quality of the landscape due to the "...synergistic effect of each landscape component on the others..." (Danielson 1992: 408). Another point to consider when incorporating more habitat types into the model is the effect of searching costs on animals dispersing through a landscape that contains a variety of habitat types (Danielson 1992). How much time and effort an individual will invest in finding the best site may depend on how much fitness is lost to dispersal (see Morris 1992).

Patches of usable habitat may imply that these patches are of some minimum size. However, there may be patches that are so small as to be unusable even though they are otherwise similar to larger, usable patches. These small patches, hereafter called "micropatches," are much smaller than an individual's home range, and perhaps could be lumped into the matrix. Alternatively, the micropatches may have other functions from the perspective of an individual animal such as increasing the survival rate of animals moving between patches.

Because of its small size, the micropatch is unusable in terms of reproduction, but it may nonetheless be important. For example, micropatches may be resource-providing patches for an organism seeking shelter from a predator. Second, used as a stepping stone, the moving animal may forage briefly or rest before moving on to search for a larger habitat patch. Third, micropatches may simply augment the value of the nearby habitat patches. Of these three potential functions of micropatches, the first two reduce the cost of movement

through a fragmented landscape while the third function is one of simple resource enrichment.

Our objective is to determine whether the presence of very small micropatches affects the ways in which mice use larger habitat patches. In our study, usable patches for *P. leucopus* are patches of woody vegetation (*Cornus* species) on the order of 2500 m^2. Home ranges for this species range from 1000—5000 m^2 (Stickel 1968, Lackey et al., 1985). Micropatches are very small clumps or individual *Cornus* shrubs and are several orders of magnitude smaller (2-3 m^2 in size). *P. leucopus* do not permanently reside in them. We predict that the presence of a micropatch will influence an organism's locomotor behavior, and promote habitat selection through increased movement within a patchy landscape. Specific hypotheses addressed were: 1) by decreasing the costs of movement between patches, micropatches will reduce environmental heterogeneity among nearby habitat patches. 2) The presence of a 'destination' patch beyond a group of micropatches may increase the use of micropatches by *P. leucopus*, making the micropatches more valuable. 3) Because micropatches are so small, they may represent pure edge habitat without any core area. 4) An individual's home range is more likely to span multiple patches if there are intervening micropatches between them.

We used live trapping and behavioral measures of foraging for seeds to measure habitat use and environmental quality. Foraging behavior can be quantified by the rate of food intake when the animal leaves a given patch. This is termed a giving-up density (GUD). Using GUDs assumes that an animal will leave a food source when the benefits of continued feeding at the source no longer exceed the benefits of foraging elsewhere in the environment

(Brown 1988). Optimal foraging theory (Stephens and Krebs 1986) and Charnov's marginal value theorem (1976) provide the formal framework behind this reasoning. While foraging, an animal's harvest rate may decline as local food density declines. Thus, the animal eventually reaches a point where the marginal benefits of continued harvest drop to equal the marginal costs (e.g. energetic costs of foraging, cost of predation, and cost in terms of missed foraging elsewhere in the environment). If the animal continues to exploit the food source, its costs will eventually exceed its benefits. Instead, the animal stops harvesting and leaves. The density of food at this point is the giving-up density (GUD). It provides a measure of habitat quality (high GUDs indicate high habitat quality and low GUDs indicate low quality). Differences in quality among patches are due to variation in the amounts of available food and foraging costs (Brown 1988) or to the patch's accessibility to the animal (Evans 1981). GUDs have also been used to assess habitat usage for many species of small mammals (Kotler and Brown 1990, Abramsky et al., 1990, Kotler et al., 1993, Kotler and Blaustein 1995, Holtcamp et al., 1997).

Methods

Study Site

We conducted our study from May to August of 1998 and 1999 at Camp Dodge Military Reserve, Polk County, Iowa. The military installation is composed of many habitat types, including old-field grassland dominated by cool-season grasses, reconstructed wetlands, warm-season grassland, and tracts of hardwood forest. The area is managed by the US Army Corps of Engineers, who have recently focused their attention on the maintenance of biodiversity in this managed area. Our study sites were located in areas containing

fragments of shrub habitat where small mammals, such as *Peromyscus leucopus*, exist. These woody fragments range from 2 to 40,000 m^2. The matrix surrounding these fragments is comprised of old-fields dominated by grasses such as brome (*Bromus inermis*) and bluegrass (*Poa pratensis*). This highly fragmented area contained discrete patches of habitat, providing arrangements of micropatches and larger patches which *P. leucopus* can use in their foraging bouts. The distances between these patches are relatively short (10—100 m), allowing us to test our predictions well within the home range of the mice (1000—5000 m^2; Stickel 1968, Lackey et al., 1985).

In addition to the white-footed mouse (*P. leucopus*), we observed meadow voles (*Microtus pennsylvanicus*), prairie voles (*M. ochrogaster*), western harvest mice (*Reithrodontomys megalotis*), and eastern chipmunks (*Tamias striatus*). Although all of these small mammals are potential seed predators, we removed the chipmunks and the harvest mice whenever we live-trapped them. While voles were abundant in the fields near the study sites, they tend to be excluded from the shrub habitat by the white-footed mouse (Grant 1972, Bowker and Pearson 1975, M'Closkey 1975), and from the trays, owing to their slightly elevated entrances. Voles also depend principally on foliage, rather than seeds, as their primary food (M'Closkey and Fieldwick 1975).

Experimental design

Six replicates of three "treatment" patch arrangements were established in blocks with one replicate of each treatment per block throughout the northern section of Camp Dodge. Within each block, the three treatments were located randomly for a total of 18 sampling units. Each treatment consisted of woody habitat patches, micropatches, and the matrix. Large habitat patches ranged from 2000—10,000 m^2 while micropatches were never larger

than 5 m^2. The distance between the two large patches ranged between 20-60 m (Table 1) and is within a mouse's home range (1000—5000 m^2; Stickel 1968, Lackey et al., 1985). A buffer of at least 50 m of old-field grassland separated each treatment plot from each other and from any other woody fragments. A description of each treatment is discussed in the micropatch pattern section below.

The giving-up density (GUD) trials were conducted during July and August in 1998 and May through July in 1999. Clear plastic water jugs (7.6 liters) containing a mixture of 1 liter of sand mixed with 3 grams of white millet seed (approximately 40 seeds) were placed in each patch of the treatment plots (see Fig. 1). The jugs (hereafter referred to as seed trays) were approximately 21.5 by 24 cm in length and width and 16 cm high. Entrance to the tray was through a 9 cm opening. Any difference between the initial seed density (3 g/l) and the GUD would show us if the tray was visited, and comparing GUDs between different patches measures patch use and environmental quality.

One seed tray was placed in each of the two micropatches while two trays were placed in each of the larger habitat patches in each of the treatments (Fig. 1). In Treatment 1, which contained no micropatches, two seed trays were placed in the matrix habitat midway between the larger habitat patches. Treatment 2 contained only one large habitat patch, but two seed trays were placed in the matrix habitat on the other side of the micropatches (Fig. 1).

A preliminary test of diminishing foraging rates in the trays was performed during 1998 to determine that two days were required before *P. leucopus* reached their giving-up-density. After two days, we sifted the seeds from the sand and replenished the trays with a fresh set of seeds. In addition, notes of tail drags in the sand and presence of fecal matter

were used to determine which species visited the trays. Tail drags indicated foraging *P. leucopus* while large feces indicated the presence of *T. striatus*; we discarded the GUDs from the *T. striatus* trays. Collected seeds were dried in an oven (65° C) and their dry weights were measured. We conducted 4 trials during the summer of 1998 for a sample size of 48 while a sample size of 142 was generated in 1999 from 12 trials.

Measuring habitat quality with GUDs

To test whether the GUDs quantify environmental quality, we conducted an enrichment study in 1999. Two seed trays were placed in each of 12 pairs of patches in Treatments 1 and 3 (each patch separated by less than 40 m). In one patch of each pair, we added 9 petri dishes, each containing ~ 20 g of millet seeds. The 9 petri dishes were arranged in the same manner as the traps shown in Fig. 1. We compare GUDs between the supplemented and unsupplemented patch in each pair using randomized block ANOVA for multiple comparisons.

Effects of micropatches in reducing inter-patch heterogeneity

To test whether micropatches influence the traffic or 'evenness' with which habitat is exploited, we compared GUDs and live trapping results in two treatments that we referred to Treatment 1 and Treatment 3. Treatment 1 consisted of pairs of habitat patches (> 2000 m^2) with no micropatches in between. Treatment 3 consisted of similar pairs of patches with two or more micropatches between them. In each patch, we calculated an average GUD from the two seed trays (Fig. 1). Then, for each pair of patches (A and C in Fig. 1) in both treatments, we calculated the absolute difference of their average GUDs. These differences were then compared with a Student's t-test for paired data (since each treatment occurred in each block).

A destination to promote movement

To determine if the presence of a "destination" patch beyond the micropatches affects the use of the micropatches, we compared GUDs in the two micropatches in Treatment 3 (described above) to GUDs in two micropatches in Treatment 2. Each replicate of Treatment 2 contained only one patch and a cluster of micropatches (Fig. 1), and thus, any mice using the micropatches in Treatment 2 were not doing so incidentally to traveling to another suitably large patch. These micropatch GUDs were compared with randomized block ANOVA for multiple comparisons.

Edge-effect patterns

To examine potential within-patch edge effects, two trays were placed in each large fragment patch in each trial: one close (<1 m) to the edge nearest the micropatches, and one near the center of the patch (Fig. 1). We used Treatments 1 and 3 to test this aspect. We also wished to determine if micropatches might be perceived as edge habitat. To this end, we compared the GUDs from the edge of each patch in Treatment 3 to the GUDs in the micropatches in Treatment 3 using a randomized block ANOVA for multiple comparisons.

Micropatches to promote home-range expansion

To determine if micropatches promote home ranges spanning multiple patches of suitable habitat, we established trapping grids of 9 Sherman live-traps within the patches of each treatment. For Treatment 2, consisting of only one patch, a 9-trap grid was also established in the grassy-matrix area ~ 47 meters away (Fig. 1). One trap was placed in each of two micropatches in Treatments 2 and 3, and two traps were placed in the matrix between the two patches in Treatment 1 (location B in Fig. 1). In each grid, traps were 5 m apart and baited with oats. Traps were prebaited for 2 days prior to each trapping session. Trapping

was conducted for 4-day sessions in June and August in 1998 and June and July in 1999. Trapping sessions were organized to avoid overlap with the collection of GUD data. Traps were set in the afternoon and checked the next morning. Captured animals were identified, sexed, weighed, marked with an ear-tag for future identification, and released. We compared the number of individual mice that moved between the A and C grids (Fig. 1) in each treatment using a randomized block ANOVA for multiple comparisons.

Results

Manipulation of habitat quality

Before proceeding to test the micropatch hypotheses, we wanted to make sure that the GUDs can be used as an indicator of environmental quality. We predicted that the GUDs in the enriched patch (containing more seeds) should be higher than those in the poorer quality patch. Both Treatments 1 and 3 showed significantly higher GUDs in the enriched patch (treatment 1: $p = 0.004$; treatment 3: $p = 0.009$; Fig. 2).

Effects of micropatches in reducing inter-patch heterogeneity

We wish to determine whether micropatches aid mice in moving between larger patches of suitable habitat. If this were true, we would expect the average differences of the GUDs in the A and C patches in Treatment 1 to be greater than the average difference between the same patches in Treatment 3 (see Fig. 1). These differences were calculated by using:

$$\frac{\sum_{j=1}^{i} |GUD_{jA} - GUD_{jC}|}{i} \qquad (1)$$

where i = number of trials and j = treatment. In 1998, our results showed no significant difference between the two treatments ($p = 0.09$, n=48; Fig. 3). In 1999, there was a significant difference in the GUDs ($p = 0.01$, n=142; Fig. 3) between the two treatments. However, note in Fig. 3, Treatment 3 exhibited a higher difference than Treatment 1. This difference is directly opposite our prediction.

A destination to promote movement

Perhaps micropatches may be viewed as additional habitat. Alternatively, they may simply be stepping stones in a fragmented landscape. As stepping stones we would anticipate heavier use (and thus lower GUDs) of micropatches that lie between patches of suitable habitat than in micropatches that do not lie en route to a larger destination patch. By comparing the GUDs in the micropatches of Treatments 2 and 3, we can determine whether the presence of a "destination" patch might affect a mouse's behavior to move through the micropatches. If there is no place for the mouse to move to, it may not use the micropatches as readily.

In 1998, there was no significant difference in the use of micropatches between Treatments 2 and 3 ($p = 0.87$; Fig. 4). However, in 1999, the difference was highly significant ($p < 0.01$; Fig. 4). The dissimilarity between years may have been due to the much smaller sample size in 1998 (n = 48, 1998; n = 142, 1999) and to the fact that there were fewer mice in 1999 (see below). GUDs in the micropatches in Treatment 2 were higher than those in Treatment 3, suggesting that in the absence of a destination patch, a mouse may be more reluctant to use the micropatches in Treatment 2.

Micropatch promotion of multi-patch home ranges

Micropatches may be of value in allowing the home ranges of individual mice to span multiple patches of suitable habitat. Figure 5 illustrates the average number of movements (between A and C trapping grids) that occurred in the two 4-day trapping sessions in each treatment for both 1998 and 1999. Here, we define movement as any instance in which a marked individual is recaptured in a trapping grid (A or C; Fig.1) other than the grid where it was last captured. Comparisons between Treatments 1 and 2 yielded no significant differences during both 1998 and 1999 movement rates ($p = 0.48$, 1998; $p = 0.9$. 1999; Fig. 5). A significant difference was detected when comparing Treatment 3 to either Treatment 1 ($p = 0.02$, 1998; $p = 0.05$, 1999; Fig. 5) or Treatment 2 ($p = 0.01$, 1998; $p = 0.05$, 1999; Fig. 5). Combined with the findings from the above comparisons, our results seem to indicate that micropatches promote movement through a fragmented landscape, regardless of the presence of another source patch.

In 1998, more *P. leucopus* were captured (180 individuals) than in 1999 (83 individuals). We also found that male *P. leucopus* tended to move more than females (1998: 25 males, 9 females; 1999: 9 males, 2 females). No significant differences were found between males who moved in Treatment1 and those in Treatment 3 either 1998 or 1999 (t-test; $p=0.22$, 1998; $p=0.45$, 1999).

Edge-effect patterns

Micropatches may be thought of as small fragments of edge habitat. However, edges of our larger patches may be of greater value to the mice because of their proximity to a core area. Treatment 1 GUDs at edges were lower than GUDs in the interior of the patches in 1998, but not significantly so ($p = 0.18$; Fig. 6). In 1999, GUDs on edges were significantly

lower than interior GUDs ($p < 0.01$; Fig. 6), although the magnitude of the difference was less than in 1998. Treatment 3 GUDs did not show any edge effects in either 1998 or 1999 ($p = 0.81$, 1998; $p = 0.90$, 1999; Fig. 7).

When comparing the edge GUDs to those in the micropatch in Treatment 3, we did not detect any significant difference in either 1998 or 1999. While *P. leucopus* is perceived as an edge species (Geier and Best 1980), both our larger patches and the micropatches are so small as to be, perhaps, homogeneous edge habitat.

Discussion

Manipulation of habitat quality

Brown (1988) originally developed the concept of measuring the amount of seed remaining in seed trays (giving-up densities) as a function of predation risk and foraging costs. Since then, others have used giving-up densities to measure environmental factors (Kotler et al., 1993), interspecific competition, and species coexistence (Abramsky et al., 1990, Kotler and Brown 1990). We demonstrated that GUDs can be used as a barometer of environmental quality. GUDs can be used as empirical evidence of how foragers are responding to changes in environmental quality such as enriching the habitat with additional resources such as food or cover. As Brown (1999) has modeled in a recent paper, GUDs should increase with increasing predation risk. Environmental quality can replace predation risk in the same model, which then predicts that richer environments will have higher the GUDs than poorer environments. Foragers no longer have to forage as long or hard in the seed trays because high-quality habitats contain more food or other resources. Adding more

seeds to the habitat patches, thus enriching the environment, increased the GUDs substantially (Fig. 2).

The function of micropatches

Peromyscus leucopus may view a patchy landscape as containing a series of habitats. The species has a penchant to travel 200—300 m during a foraging bout (Stickel and Warbach 1960; Orniston 1983). Thus, the animal is easily capable of traveling between multiple patches in the landscape. In doing so, it may utilize micropatches as additional habitat in which to forage. Alternatively, it may use micropatches as resting or cover locations along its path. And, of course, micropatches may serve both functions. Clearly, the GUDs indicate that the mice forage in the micropatches. In all cases, micropatch GUDs were less than 1.5 (from an initial level of 3.0), indicating that over half of the millet seed was removed. Furthermore, there was only slightly greater use of micropatches in 1999, when there was a destination patch (Treatment 3; Fig. 4). This suggests that the micropatches may be thought of as additional habitat that supplements the larger patches.

Do micropatches represent edge habitat, by virtue of their size? Before answering this question, we must define habitat edges. Formally, habitat edges are discontinuities in habitat features perceived by a focal individual or species that in turn affects its performance in some way (Lidicker 1999). Performance can be measured in behavioral, physiological, or demographic terms. Whether positive or negative, habitat edges produce a multitude of effects. However, no significant difference in *P. leucopus* performance was found between the micropatches and either the interiors or the edges of the larger patches in Treatment 3 (Fig. 7). This suggests that there are only two types of habitat in our experimental landscapes – suitable habitat patches and unsuitable matrix habitat.

Perhaps the large habitat patches in our experiments were not big enough for *P. leucopus* to perceive them as being composed of both edges and interior. Geier and Best (1981) and Manson et al. (1999) suggest that *P. leucopus* are edge-philic, and thus both the larger patches and the micropatches represent homogeneous edge habitats to the mice.

Micropatches clearly appear to be important to mice moving between patches, as evidenced by the substantially greater number of movements per individual between neighboring patches when micropatches are present (Fig. 5). This apparent freedom of movement should produce greater homogeneity of habitat quality among patches. According to the ideal-free distribution (Fretwell and Lucas 1970), individuals that are free to move among patches should assort themselves so that the expected fitness of individuals is constant across the habitat spectrum. This distribution should, in turn, result in reducing resources to the same levels in all otherwise similar patches. Our results show that while mice may be moving more between the large patches (Fig. 5), they are not foraging equally across the landscape (Fig. 3); where mice have the greatest freedom of movement (Treatment 3) they produce the greatest heterogeneity in GUDs (Fig 3). This is in direct contrast to the predictions of the ideal-free distribution model and to other studies of density-dependent habitat selection in *P. leucopus* (Morris 1989, Morris 1991). We have no explanation of the apparent contradiction other than speculation that the paired A and C patches in Treatment 3 may have been, in some unknown way, more heterogeneous than the A and C patches in Treatment 1. This does not seem likely.

Nevertheless, micropatches appear to be important in linking patches in heavily fragmented landscapes. And thus, micropatches that are much smaller than the home range of a single individual may be important in evaluating the general quality of a fragmented

landscape for supporting a population that predominantly resides in the larger fragments. There may be no patch of habitat that is so small as to be valueless to the welfare of the population.

Literature Cited

Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Kotler, B. and Mitchell, W.A. 1990. Habitat selection: An experimental field test with two gerbil species. Ecology. 71: 2358-2369.

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius*. Ecology. 71: 355-366.

Bowker, L.S. and Pearson, P.G. 1975. Habitat orientation and interspecific interaction of *Microtus pennsylvanicus* and *Peromyscus leucopus*. Am. Midl. Nat. 94: 491-496.

Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. and Sociobiol. 23: 27-43.

——. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol. Ecol. Res. 1: 49-71.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Pop. Biol. 9: 129-136.

Cummings, J.R. and Vessey, S.H. 1994. Agricultural influences on movement patterns of white-footed mice (*Peromyscus leucopus*). Am. Midl. Nat. 132: 209-218.

Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evol. Ecol. 6: 399-411.

Dunning, J.B., Danielson, B.J. and Pulliam, R.H. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.

Evans, R.M. 1982. Efficient use of food patches at different distances from a breeding colony in black-billed gulls. Behaviour 79: 28-38.

Fretwell, S.D. and Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19: 16-36.

Geier, L.L. and L.B. Best. 1980. Habitat selection by small mammals of riparian communities: Evaluating effets of habitat alteration. J. Wildl. Manage. 44: 16-24.

Gilpin, M.E. and Hanski, I. 1991. Metapopulation dynamics. Academic Press, New York.

Gottschang, J.L. 1981. A guide to mammals of Ohio. The Ohio State University Press, Columbus. 176 p.

Grant, P.R. 1972. Experimental studies of competitive interaction in a two-species system. J. An. Ecol. 40: 323-335.

Kaufman, D.W., and E.D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. So. Nat. 18: 443-452.

Kotler, B.P. and Brown, J.S. 1990. Rates of seed harvest by two species of gerbilline rodents. J. Mammal. 71: 591-596.

Kotler, B.P., Brown, J.S. and Mitchell, W.A. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. J. Mammal. 74: 614-620.

Lidicker, W.Z., Jr. 1999. Responses of mammals to habitat edges: An overview. Land. Ecol. 14: 333-343.

MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Manson, R.H., Ostfeld, R.S. and Canham, C.D. 1999. Responses of a small mammal community to heterogeneity along forest-old-field edges. Landscape Ecol. 14: 355-367.

M'Closkey, R.T., and B. Feldwick. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). J. Mammal. 56: 119-129.

Milne, B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. Am. Nat. 139: 32-57.

Morris, D.W. 1989. Density-dependent habitat selection: testing the theory with fitness data. Evol. Ecol. 3: 80-94.

——. 1991. Fitness and patch selection by white-footed mice. Am. Nat. 138:702-716.

——. 1992. Habitat selection and patch size in heterogeneous prairie landscapes. Evol. Ecol. 6: 412-32.

Palmer, M.W. 1992. The coexistence of species in fractal landscapes. Am. Nat. 139: 375-397.

Pickett, S.T.A. and White, P.S. (eds) 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652-661.

Stephens, D.W. and Krebs, J.R. 1986. Foraging Theory. Princeton University Press, Princeton, NJ.

Shorrocks, B. and Swingland, I.R. (eds) 1990. Living in a patchy environment. Oxford University Press, Oxford.

Stamps, J.A., Buechner, M. and Krishnan, V.V. 1987. The effects of edge geometry on territorial defense costs: intruder pressure in bounded habitats. Am. Zoo. 27: 307-325.

Wegner, J.F. and Merriam, G. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. J. App. Ecol. 27: 879-890.

Wiens, J.A., Crist, T.O, With, K.A. and Milne, B.T. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology 76: 663-666.

With, K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecol. 9: 25-36.

With, K.A. and Crist, T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

With, K.A, Gardner, R.H and Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151-169.

Table 1. Average distances between the large habitat patches, micropatches, and the matrix habitats among replicates for each treatment. A total of 6 replicates for each treatment. A guide to the location letters can be found in Figure 1.

Landscapes	**Patch to micropatch or matrix (loc. A–B)**	**Patch to patch or matrix (loc. A–C)**
Treatment 1	15 m	36 m
Treatment 2	20 m	47 m
Treatment 3	15 m	40 m

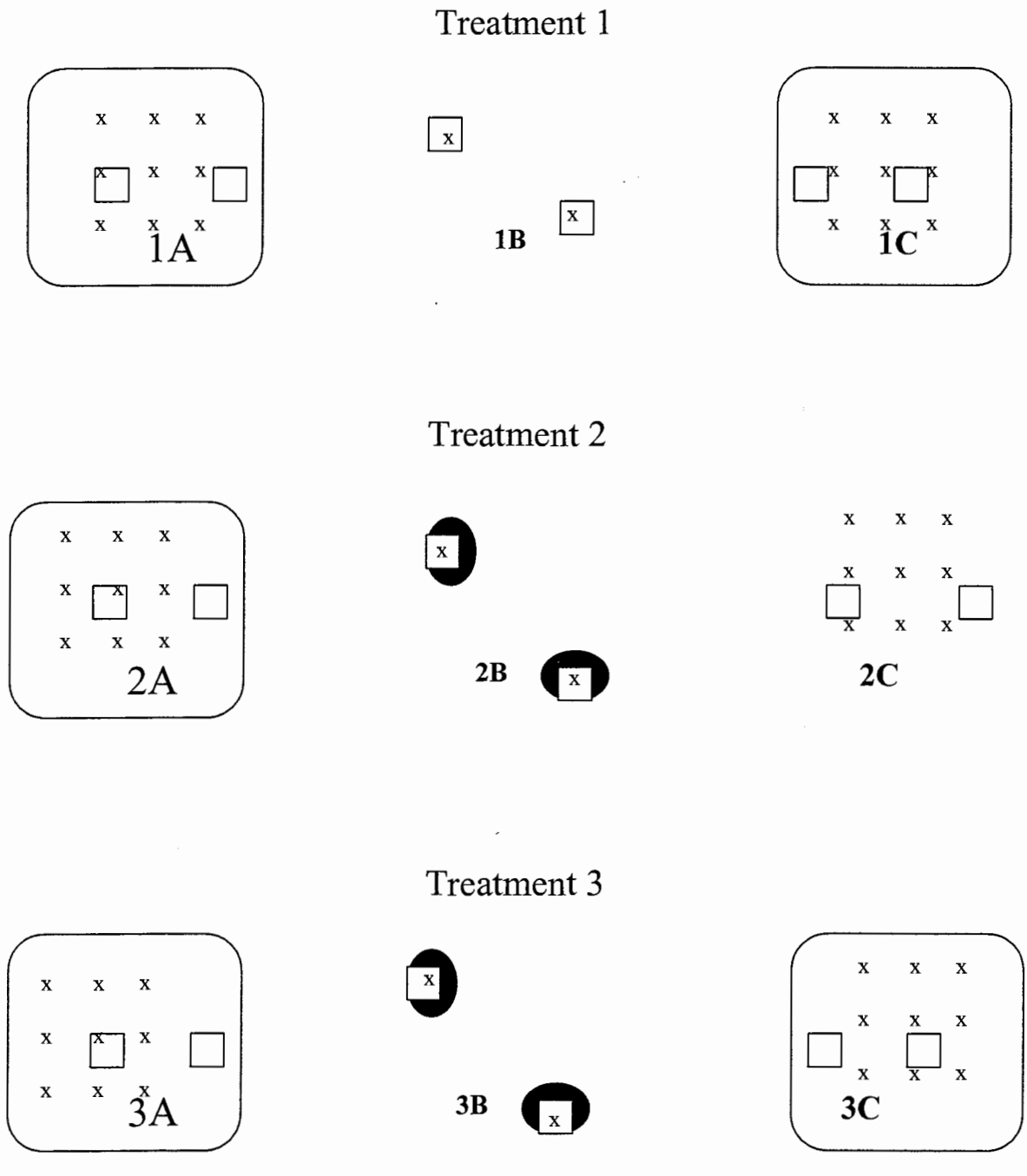


Figure 1. The treatment plots. The smaller squares represent the seed trays while the small darkened circles are the micropatches. Each patch location is labeled either A, B, or C. The seed trays and patches are not to scale. Trap grids (9 x9) are indicated by the x's and located randomly within the patches or around the seed trays. The trap sessions did not coincide with the GUDs study. There were six replicates of each treatment .

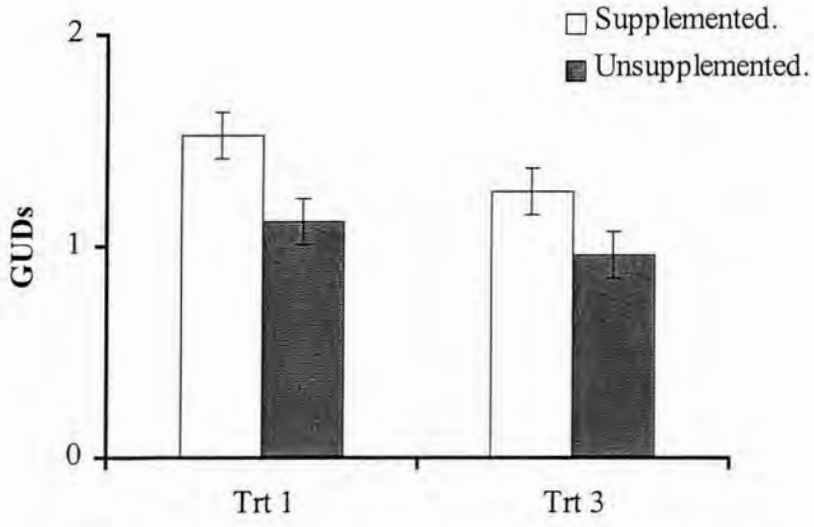


Figure. 2. Food supplementation increases GUDs, reflecting higher patch quality in the supplemented than in the unsupplemented patches. Comparisons within each treatment resulted in significant increases (treatment 1: $p < 0.001$; treatment 3: $p < 0.009$; $n = 24$).

$$\frac{\sum_{j=1}^{i} |GUD_{jA} - GUD_{jC}|}{i}$$

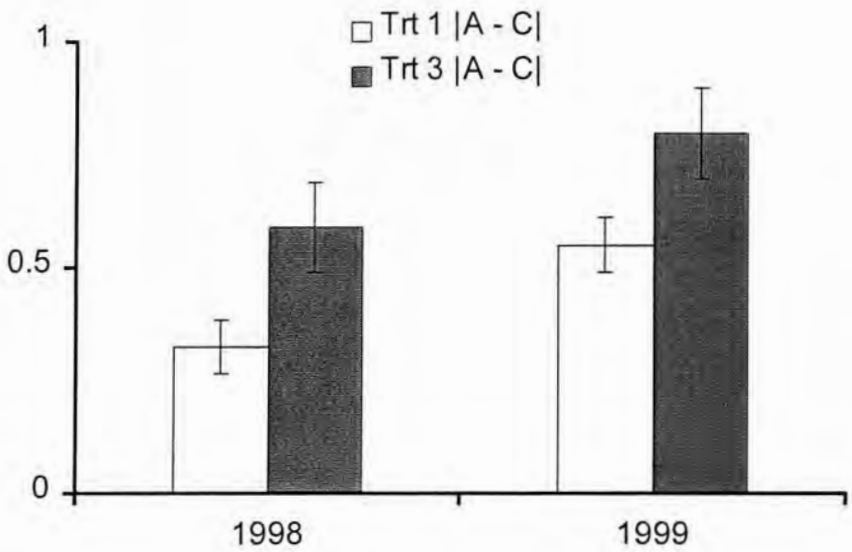


Figure 3. The average GUD difference between the two large habitat patches were compared for both treatments 1 and 3. The average GUD difference was calculated by the above equation: i = replicates; j = treatment; A - C = the difference between patch locations from Figure 1. Paired t-tests were used to compare these differences. A marginal difference was found between the two treatments in 1998 ($p > 0.09$; $n = 48$), while a significant difference was detected in 1999 ($p < 0.01$; $n = 142$).

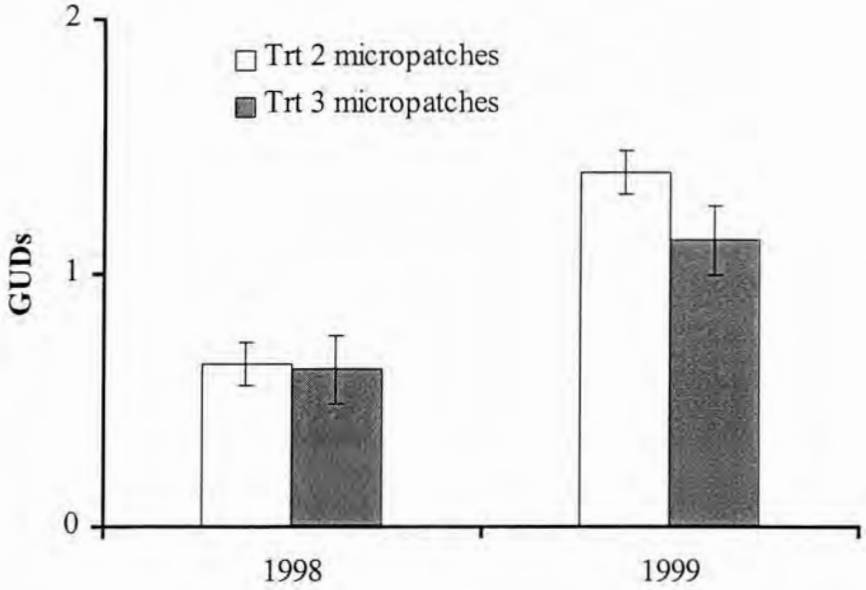


Figure 4. Comparing the micropatches between treatments 2 and 3 yielded mix results. No significant difference between the treatments was detected in 1998 ($p > 0.87$; ANOVA contrasts; $n = 48$), while a significant difference was found in 1999 ($p < 0.0001$; ANOVA contrasts $n = 142$).

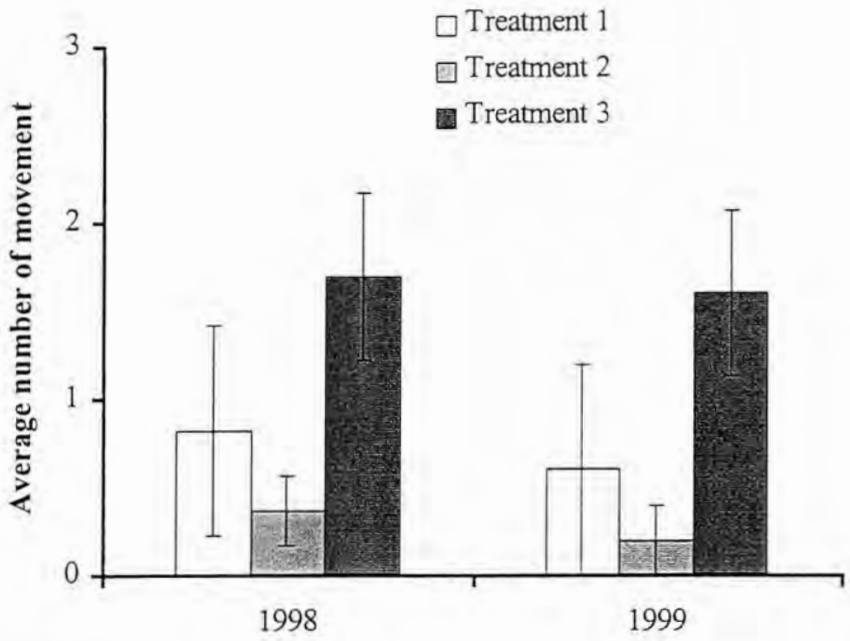


Figure 5. The average number of movement by an individual in each treatment landscape. Recall that Treatment 1 contains no micropatches while Treatments 2 and 3 do. No significant results were found when comparing treatments 1 and 2 (1998: $p > 0.48$; 1999: $p > 0.9$). We found significant differences between treatments 1 and 3 (1998: $p < 0.02$; 1999: $p < 0.05$). Significant differences were also found between Treatments 2 and 3 (1998: $p < 0.02$; 1999 $p < 0.05$).

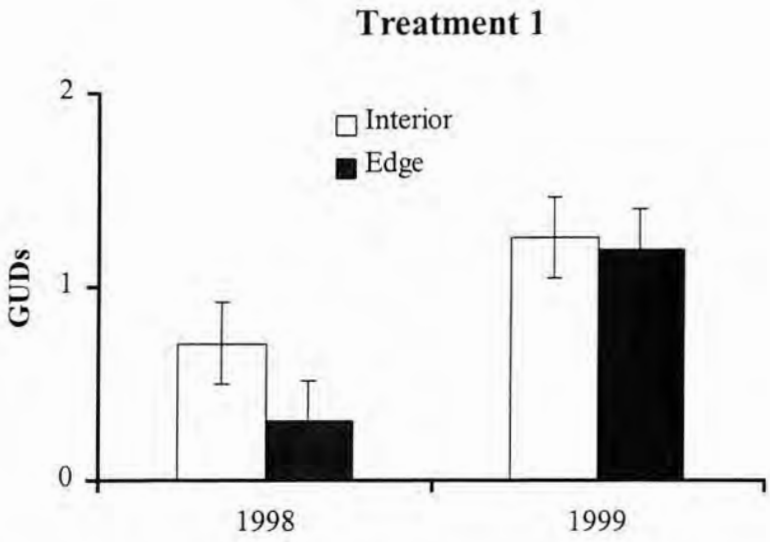


Figure 6. In testing if interior habitats are similar to the edge habitat of larger patches in treatment 1, we did not detect any differences in 1998. However, with a larger sample size in 1999, we detected a significant difference between the interior and edge habitat of large habitat patches ($p < 0.0001$). We also detected differences between the interior habitat and the grassy matrix ($p < 0.001$). All comparisons made using ANOVA contrasts; 1998 $n = 48$; 1999 $n = 142$.

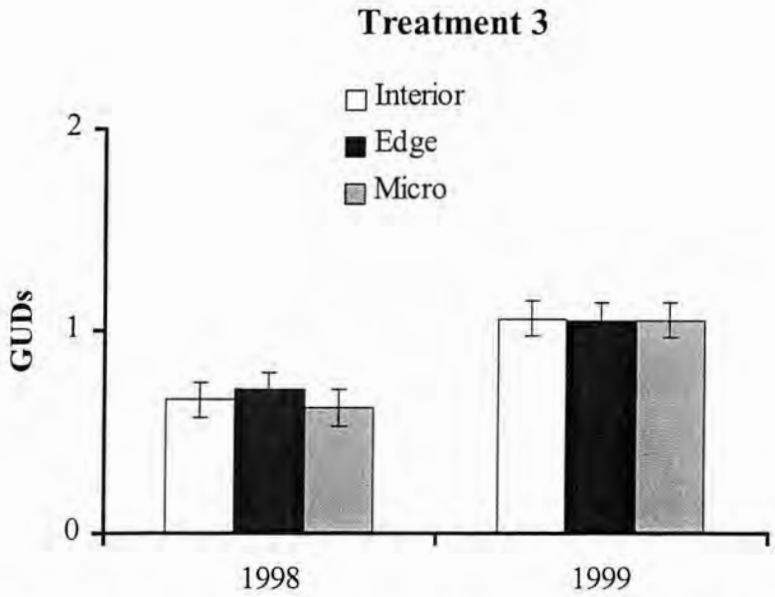


Figure 7. We compared the edge, interior, and micropatch habitats for treatment 3. We did not detect any significant differences among the three habitat types during 1998 or 1999 ($p > 0.05$ for all comparisons using ANOVA contrasts). 1998 $n = 48$; 1999 $n = 142$.

CHAPTER 4: GENERAL CONCLUSIONS

General Discussion

Habitat loss and fragmentation are among the most pervasive threats to the conservation of biological diversity (Wilcove et al. 1986, Wilcox and Murphy 1985). Iowa, containing less than 0.02% of pre-settlement prairies (Smith 1981), provides conservation biologists and ecologists an opportunity to investigate the effects of habitat loss and fragmentation on its flora and fauna.

We found one state-endangered species, the plains pocket mouse (*Perognathus flavescens*), as well as the rarely observed least weasel (*Mustela nivalis*) in Camp Dodge, Iowa. These species are examples of animals that are on the edge of their geographic range. Because Camp Dodge contains large contiguous grassland habitats, camp personnel can manage their training areas to attract and maintain the presence of these species.

A negative relationship between two herbivores occupying similar habitats (*Microtus ochrogaster* and *Microtus pennsylvanicus*) was detected. Like some investigators studying small mammal grassland species in the Midwest (Getz et al. 1987; Zimmerman 1965), we attribute this trend to differences in habitat preference. Grassland granivores (*Peromyscus maniculatus* and *Reithrodontomys megalotis*) also exhibited a similar negative relationship where they occurred. Because many areas in the Camp are burned annually, litter levels are reduced. Kaufman et al. (1988), found *P. maniculatus* to respond positively to low levels of ground litter. Our data suggest the same tendency for *P. maniculatus* when selecting their habitat. Kaufman et al. (1988) also attribute the negative correlation between *R. megalotis* and *P. maniculatus* to interspecific competition. *P. maniculatus* is the bigger granivore and could easily out-compete the smaller *R. megalotis*.

Agricultural mowing is a necessary practice on Camp Dodge in order to keep its extensive grasslands. However, we found mowing to affect the abundances of small mammals negatively. We suggest that a rotational schedule may alleviate the loss of vegetation that seems to affect these small mammals.

In addition to the vast expense of grasslands, highly fragmented patches of woodland habitat comprise the rest of Camp Dodge. This area provided us the opportunity to test whether small fragments of habitat may influence how an organism uses the rest of the habitat patches. Small fragments, referred to hereafter as micropatches, are so small that they may seem useless to the organism. However, we found that micropatches supplement the patchy landscape by providing *Peromyscus leucopus* additional habitat in which they forage. Additionally, by connecting larger patches of habitat, micropatches promoted the use of multiple patches. *P. leucopus* moved more readily when micropatches span between large patches of habitat.

Habitat fragmentation often leads to the isolation of small populations and ultimately reduction in biological diversity (Pimm et al., 1988). The inclusion of corridors or stepping stones in reserve designs has become an important conservation tactic for protecting biological diversity (Rosenberg et al., 1997). As wildlife habitat and biological corridors, linear or patches of habitat fragments may serve important roles in linking the landscape even as it becomes increasingly fragmented.

Literature Cited

Zimmerman, E.G. 1965. A comparison of habitat and food of two species of *Microtus*. *Journal of Mammalogy* 46: 605-612.

Getz, L.L., J.E. Hofman, B.J. Klatt, L. Verner, F.R. Cole, and R.L. Lindroth. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *Microtus pennsylvanicus* in east central Illinois. *Canadian Journal of Zoology* 65: 1317-1325.

Kaufman, G.A., D.W. Kaufman, and E.J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. 1988. *Journal of Mammalogy* 69:342-352.

Pimm, S.L., H.L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757-785.

Rosenberg, D.K., B.R. Noon, and E.C. Meslow. 1997. Biological corridors: form, function, and efficacy. *Biosci.* 47:677-687.

Smith, D.D. 1981. Iowa prairie: an endangered ecosystem. *Proc. Iowa Acad. Sci.* 88:7-10.

Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. pp 237-256 *in* Soulé, M.E., ed. Conservation biology. Sunderland, MA.: Sinauer Assoc.

Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879-887.

ACKNOWLEDGEMENTS

This research was aided by a grant from the Camp Dodge National Guard Legacy Endowment and supported by Iowa State University. I would like to extend my deepest appreciation to my advisor, Brent Danielson, for his support and guidance throughout this project. I would also like to thank Rolf Koford and Steve Jungst for their comments on this project. I would like to thank Steve Hanser and Rich Olsen for their help in collecting data. I would also like to thank Jeff Jaros-Su, John Orrock, and Adam Remsen for their support and encouragement when the "going got tough" and numerous comments on the manuscripts. The comments from E.L.V.I.S. are also appreciated.